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The tracheae of salticid spiders

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THE TRACHEAE OF SALTICID SPIDERS. D. E. Hill

As noted by Lamy (1902), salticids possess very highly developed tracheae, in addition to an ample pair of book lungs.

All of these tube tracheae originate (open to the exterior) with a single slit-spiracle on the ventral midline, just in front of the spinnerets. This spiracle can apparently be closed by the action of certain muscles which insert upon its lateral processes. The spiracle opens into a single vestibular sac, which rapidly divides (Figs. 1 and 2) into two flattened air-sacs of the postero-ventral opisthosoma. These air-sacs are lined, as is the vestibular cavity of the book lungs, with an irregular reticulum of cuticular struts. The individual tracheae originate in groups (Fig. 2) from various positions along the air sacs.

In Phidippus, this general arrangement agrees with that described for Heliophanus, Ballus, and Salticus by Lamy (1902). His figures were rather

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distorted as to the positioning of the tracheae, so that the figure (Fig. 1) given here, based upon serial sections is much more satisfactory. The usual procedure for the preparation of tracheae, as noted by Levi (1967) is to boil the specimen in 10% NaOH briefly. Unfortunately such procedures remove some of the tracheae, and show little of the relationship of the tracheae to the other parts of the organism.

The greatest number of tracheae are situated in the opisthosoma for their entire length (not shown in entirety in Fig. 1). These taper with length, and gradually pass between digestive diverticulae, muscles,

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and silk glands. The delicate terminal portions of the tracheae (one is shown in Fig. 3) are generally lost in NaOH preparations. The true extent of the tracheae is not even shown in the truncated (for practical reasons) Fig. 1, and these tracheae actually loop dorsally to associate with the mass of opisthosomal digestive diverticulae.

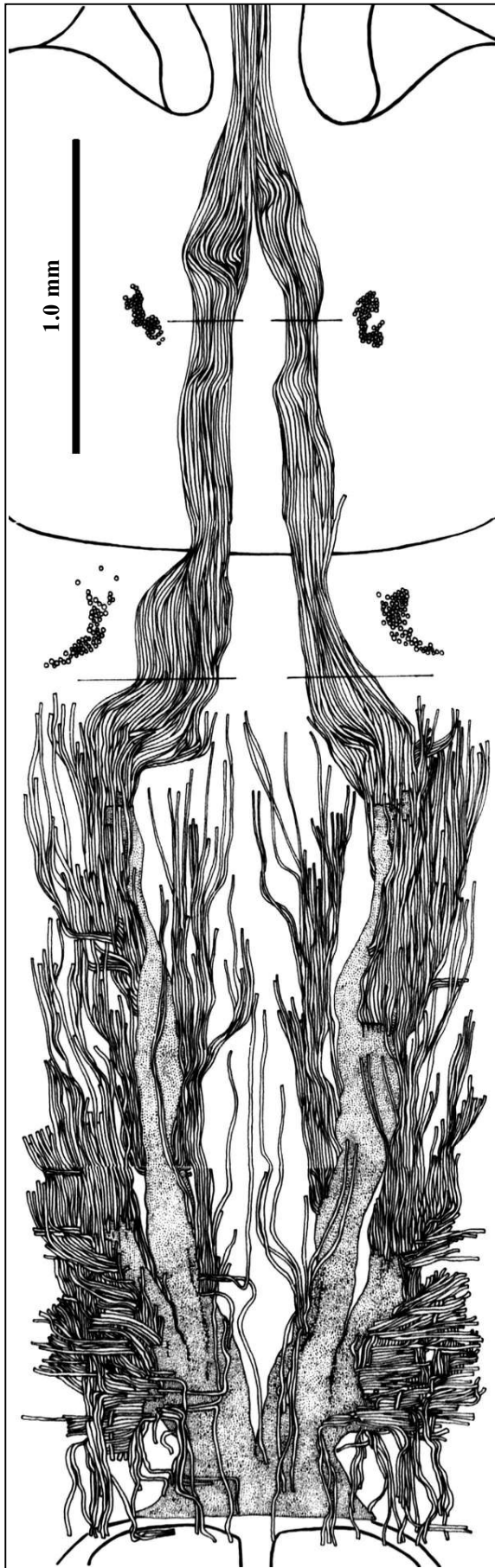
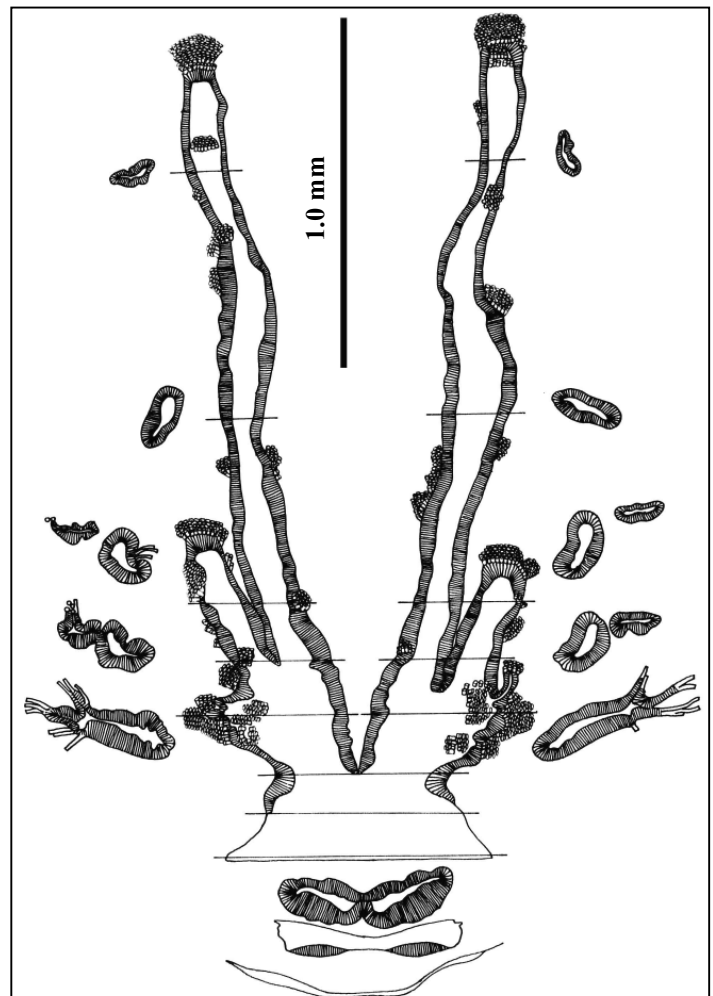


Fig. 1. (left) Reconstruction of dorsal view of air-sacs and tracheae in the opisthosoma of an adult female *Phidippus clarus* Keyserling 1884 from Corvallis, Oregon. The drawing is based upon 10 μm serial transverse sections of the entire opisthosoma. Air-sacs are stippled. The tracheal system extends from the slit-spiracle just anterior to the spinnerets on the ventral opisthosoma (bottom) to a bundle of tube tracheae associated with the opisthosomal nerves which passes through the pedicel (top) into the prosoma. Some of the latter actually pass, ventrally, between the commissures of the fused subesophageal ganglia at the midline. For reference the epigastric groove and several representative transverse sections are shown. The entire extent of the individual tracheae is not shown.

Fig. 2. (below) Reconstruction of opisthosomal air-sacs of female *Phidippus clarus*, as in Fig. 1, showing extent of unobstructed air space. The striped border of the air space represents a reticulum of cuticular struts, struts which can maintain a minimum air space within the sacs as they are compressed by opisthosomal pressure. The struts are oriented perpendicular to the wall of the air sac, as the lines indicate. The irregular hypodermis enclosing (underlying) the air-sacs, and situated between silk glands, muscles, and digestive (mid-gut) diverticulae is not shown. Representative vertical (transverse) sections are included in the diagram, and these correspond to the transverse lines on the central figure. The departure of principal groups of tracheae from the air sacs is also shown.



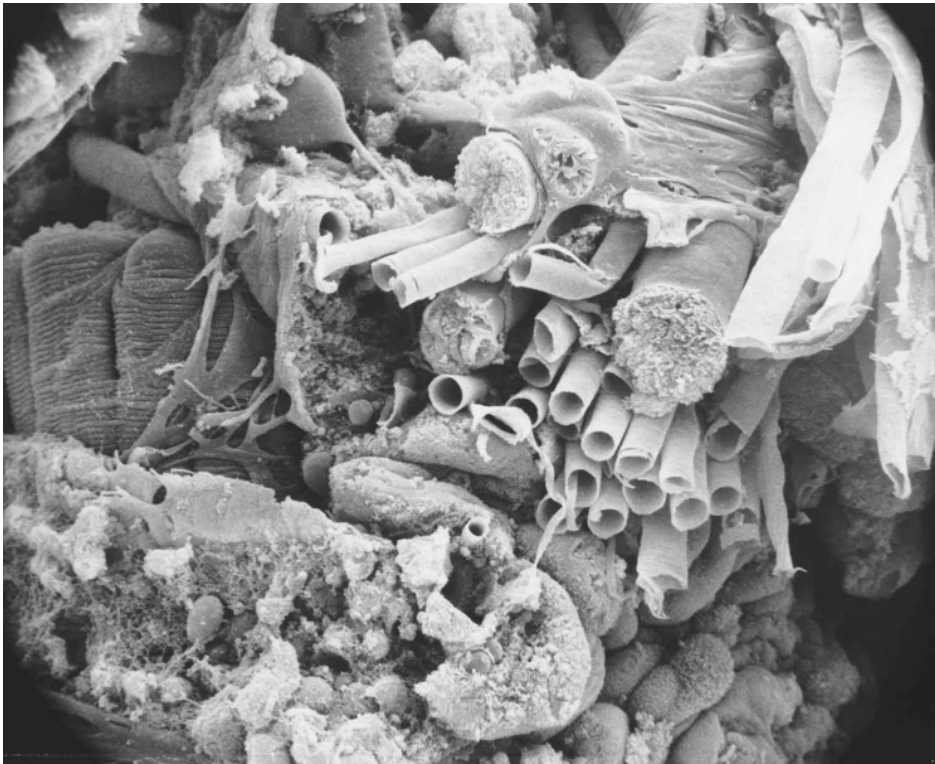


Fig. 3. Posterior SEM view of cryofractured anterior opisthosoma of adult male Phidippus audax (X 650). At left are partially contracted bundles of striated muscle, showing regular external folds. At right is a bundle of tube tracheae associated with the larger cable-like opisthosomal nerves. Note the presence of a tracheal segment of smaller diameter associated with the midgut diverticulae (lower center).

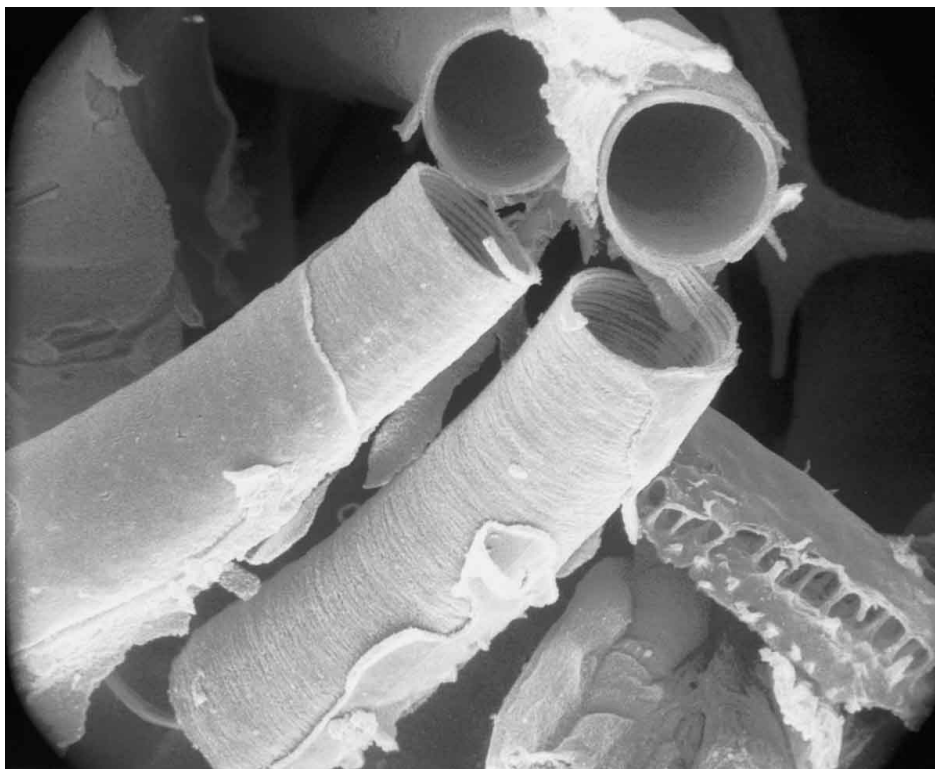


Fig. 4. Detail of cryofractured opisthosomal tracheae of adult male Phidippus audax (X 3300). The circular ribbing clearly prevents the collapse of these structures. The sheathing of the tubes is presumably cytoplasmic. For comparison, a medial portion of the book lung with fixed struts supporting the air space is shown at lower right.

Two groups of tube tracheae emerge (Fig 2.) from the anterior terminals of the air-sac, and many of these continue through the pedicel as a single group (Fig. 1). Fig. 3 shows this group of tracheae, destined for the prosoma, in association with the opisthosomal nerves. In the prosoma these are partitioned vertically. One group is apparently associated with prosomal diverticulae of the midgut above the endosternite, while the other group remains in association with nervous tissue below the endosternite.

Fig. 4 shows a detailed view of several tube tracheae, with an enveloping (presumably cytoplasmic) sheath partially intact. Moore (1976) similarly figured several tracheae of *Argyroneta aquatica*, although his methods led to the extensive distortion of all but the most resistant structures, and are definitely not to be recommended for SEM. Material for Figs. 3 and 4 was

prepared by immersion of live spiders in liquid N₂, fracture of the frozen spider with a razor, followed by standard TEM fixation, critical-point drying, and gold coating.

The function of the tracheae is clearly that of respiration, though the rationale for the existence and degree of development of these structures in spiders varies. A widely accepted justification for tracheae is that these restrict water loss while providing an adequate avenue of gaseous diffusion (Levi 1967, Levi & Kirber 1976).

Of course, as with the book-lungs of spiders, the extent to which active ventilation takes place has not been determined. The "flexible" volume of the opisthosomal air-sacs suggests that changes in local, internal opisthosomal pressure may, on occasion, have a flushing effect on the air within these sacs. This is only conjecture.

Gaseous diffusion and water conservation are plausible roles for the tracheae. Other functions suggested for the tracheae include a greater efficiency of O₂ uptake, particularly during periods of intense activity (Levi & Kirber 1976).

Clearly the presence of both well-developed book-lungs and well-developed tracheae in the same organism is problematical. If tracheae were really more efficient than the book-lungs, which I doubt, given the necessary circulation of fluids during locomotion anyway, then it would be difficult to explain the continued presence of book-lungs in salticids, which are very active spiders (high metabolic rate) by any standard. Consider also the great versatility of spiders in general in abandoning the book-lung (Levi 1967).

I propose that the presence of two different methods of respiration in salticids corresponds to two different levels of activity by these diurnal spiders. The inactive, resting spider should, for the most part, close the spiracles of the book-lungs and rely upon the tracheae for gaseous exchange with a minimum of water loss. The close relationship of most tracheae to digestive diverticulae and silk glands (opisthosomal respiration) should correlate with a sustained level of digestive metabolism and silk synthesis during this inactive period.

During periods of activity, when much more gaseous exchange is required, the book-lungs, which are coupled with the fluid medium of hydraulic activity, should come into use. Although I have not presented it in this context, there is good structural evidence for the active ventilation of the book-lungs, and these should provide the greater share of O₂ and CO₂ exchange required by the active spider. Otherwise, why would the spider abandon its program of water conservation? Clearly the book-lungs are associated with the bulk of fluid flow (hence gas transport) to the muscles involved in locomotion while most of the tracheae are confined to the opisthosoma. The use of hydraulics for locomotion suggests the further use of fluid flow for gaseous exchange.

Thus, I propose that the tracheae constitute a reserve system, for the purposes of water conservation and respiratory maintenance, during periods of inactivity. The necessity of water conservation is, in itself, evident.

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